A TAXONOMIC REVISION OF THE EASTERN AUSTRALIAN EARTHWORM GENUS *PERISSOGASTER* FLETCHER (MEGASCOLECIDAE: OLIGOCHAETA)

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Jamieson, B.G.M. 1993 06 30: A taxonomic revision of the eastern Australian earthworm genus *Perissogaster* Fletcher (Megascolecidae: Oligochaeta). *Memoirs of the Queensland Museum* **33**(1): 235-244. Brisbane. ISSN 0079-8835.

The three species assigned to *Perissogaster* by Fletcher are redescribed. Of these *P. nemoralis* and *P. queenslandica* are shown to have on each side in caudal segments a median nephridium with preseptal funnel flanked by astomate meronephridia, all nephridia being exonephric. This dichogastrin condition of the nephridia, coupled with multiplication of gizzards, is considered to warrant placing the two species in the genus *Digaster* Perrier. The trigastric condition is verified for *P. nemoralis* but *P. queenslandica* is shown to have only two gizzards. It is demonstrated for the first time that *P. excavata*, the trigastric type species of *Perissogaster*, has at least 100, mostly preseptal, nephrostomes on each side per segment caudally, a condition attributable to the Tribe Megascolecini. It is nevertheless argued that this species is closely related to *Digaster*. Parsimony analysis is equivocal between origin of *P. excavata* within *Digaster* or a sister-group relationship to the *Digaster-Didymogaster* assemblage. The latter derivation is compatible with (though not necessitating) parallel development in *P. excavata* of multiple gizzards from a monogastric ancestor with or without multiple nephrostomes. A monotypic genus *Perissogaster* is redefined for *P. excavata*.

☐ *Perissogaster, Digaster, Didymogaster, nephridia, taxonomy, parsimony analysis.*

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Perissogaster was erected by Fletcher (1887) for a new species, *P. excavata*, which differed from all known Australian oligochaetes in possessing three gizzards. Subsequently, Fletcher 1889, included *P. nemoralis* and *P. queenslandica* on the grounds that they also were trigastric.

Beddard (1895) placed *Perissogaster* and *Didymogaster* in *Digaster* because the three entities shared lobate prostates, meronephridia and more than one gizzard and were restricted to Australia. Michaelsen (1900) again separated the three genera but Sweet (1900) and Jamieson (1963) included the three species of *Perissogaster* in *Digaster* while excluding *Didymogaster*. Jamieson (1970, 1971) showed that *P. queenslandica* had dichogastrin nephridia (a stomate exonephric meronephridium median to astomate meronephridia on each side in caudal segments) and could therefore be retained in *Digaster* which has the same nephridial condition. It was, however, suggested that *P. excavata* and *P. nemoralis* should be excluded from *Digaster* in a reinstated *Perissogaster* as only astomate nephridia were demonstrated. *Perissogaster* was formally restricted to these two species by Jamieson (1975) but it was stated that the existing material of the genus was not in sufficiently good condition to allow full characterisation of the genus. The kindness of Dr Courtenay Smithers in forwarding to the author a well preserved specimen which has proved to be *Perissogaster excavata* has allowed a reappraisal of the anatomy of this species revealing an unsuspected nephridial anatomy and has prompted redescription of the types of *P. nemoralis* and *P. queenslandica* which, again, are found to differ significantly from previous descriptions.

All figures are drawn by camera lucida. The following abbreviations are used in Figs 1&2: ♀, female pore; g.m. accessory genital marking; ♂ male pore; ♀ po, male porophore; pr.d, prostate duct; pr.g. glandular portion of prostate; sp. amp, spermathecal ampulla. sp. div, spermathecal diverticulum; sp.p, spermathecal pore; v.d, vas deferens. Roman numerals indicate respective segments. Registration numbers prefixed by AMW are housed in the Australian Museum.

TAXONOMY

Perissogaster Fletcher, 1887 emend.

Type species: *Perissogaster excavata* Fletcher, 1887.

DIAGNOSIS

Setae lumbricine. Gizzards 3, in V, VI and VII; extramural calciferous glands absent. Merinephric; with numerous preseptal funnels on each side in each intestinal segment. Combined pores of a pair of tubuloracemose prostates and the vasa deferentia in XVIII. Spermathecae with pores at the anterior margins of their segments.

DETAILED DEFINITION

Setae 8 per segment; dorsal setal couple (*cd*) significantly wider than the ventral couple (*ab*). Clitellum anterior to the male pores. Combined male and prostatic pores a pair on XVIII. Accessory genital markings present. Female pores a minute pair presetally in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9.

Some preclitellar septa very strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, those in X-XII latero-oesophageal; preceding commissurals dorsoventral only; supra-oesophageal vessel oesophageal only; a pair of anterior lateroparietal trunks becoming latero-oesophageal and passing median to the dorsoventral commissurals to join the oesophageal plexus. Subneural vessel absent. Three oesophageal gizzards in V, VI and VII; extramural calciferous glands absent; intestine commencing in XVI, lacking muscular thickening, caeca and typhlosole.

Meronephric; enteronephric tufts in II-IV; astomate exonephric parietal micromeronephridia in succeeding segments but from XIV to the caudal extremity numerous preseptal nephrostomal funnels on each side in each segment; intestinal enteronephry not demonstrated. Holandric; gymnorchous; seminal vesicles in IX and XII. Prostates 1 pair, tubuloracemose. Fan shaped ovaries, and funnels, in XIII. Spermathecae short-stalked with small, sessile, lobed diverticulum.

DISTRIBUTION

New South Wales: Hawkesbury to Hunter River districts.

REMARKS

The presence of multiple nephrostomes here demonstrated for *P. excavata* for the first time, sets *Perissogaster* apart from *Digaster*, no other described characters necessitate separation of the two genera.

Perissogaster excavata Fletcher, 1887

(Figs 1A, 2A, B)

Perissogaster excavata Fletcher, 1887: 383-387.
Digaster excavata; Beddard, 1895: 486; Sweet, 1900: 123. Buchanan, 1909: 73; Jamieson, 1963: 85-90; 1971: 75.
Perissogaster excavata; Fletcher 1889: 1528; Michaelsen, 1900: 193; 1907: 162; Bage, 1910: 231; Jamieson, 1970: 44; 1975: 268-269.

MATERIAL EXAMINED

'Tuglo' property, near Mt Royal, 48km north of Singleton, under a stone on very clayey muddy soil, collector C.N. Smithers, 8 February, 1976 – 1 clitellate specimen, AMW6644. Identification checked against a badly macerated much-dissected type specimen from Morpeth, AMW 1457.

DESCRIPTION

Length = 280mm, width (midclitellum) = 16mm, greatest width (forebody) = 18mm, 175 segments (69-334mm long, 3-15mm wide, 160-195 segments; Fletcher, 1887). Form circular in cross section. Segments II and III biannulate ; remaining segments to XIV triannulate, IV weakly, the others strongly; thereafter with a strong postsetal furrow. Pigmented grey, excepting the pale ventrum, in alcohol. Prostomium proepilobous, short and broad, it and the peristomium with many longitudinal furrows. Dorsal pores absent (sometimes about 20 rudimentary pores posteriorly, Fletcher, 1889: 1528). Setae in 8 regular longitudinal rows throughout, commencing on II; minute but distinctly visible; setae *a* and *b* not visible in XVIII. In XII *aa:ab:bc:cd:dd* = 2.96:1.00:1.60: 1.50:2.68; circumference = 55mm; *dd:u* = 0.19. Nephropores not externally recognisable. Clitellum annular, XIV-XVII, with weak development to 1/2XIII and 1/2XVIII dorsally; (1/3XIII-part or most XVIII; Fletcher, 1887) intersegmental furrows and setae retained. Male pores (Fig. 1A) , from internal examination, on small indistinct elliptical papillae equatorially in XVIII in *ab* (not visible externally; Fletcher, 1887). Accessory genital markings paired presetal eye-like markings in XVIII-XXII in *bc* and a transverse glandular trough similarly located in XXIII but continuous across the ventrum; the markings in XVIII also lying in a transverse elliptical trough which impinges on the posterior region of XVII; the troughs in XVIII and XXIII with numerous longitudinal stigmata; the accessory markings and male pores lying in a rectangular flattened and thickened area. (Accessory markings limited to XVIII-XXI; Fletcher, 1887). Female pores small but distinctly visible, a pair presetally and well median of *a* lines of XIV in a common whitish glandular area which interrupts the clitellum pre-

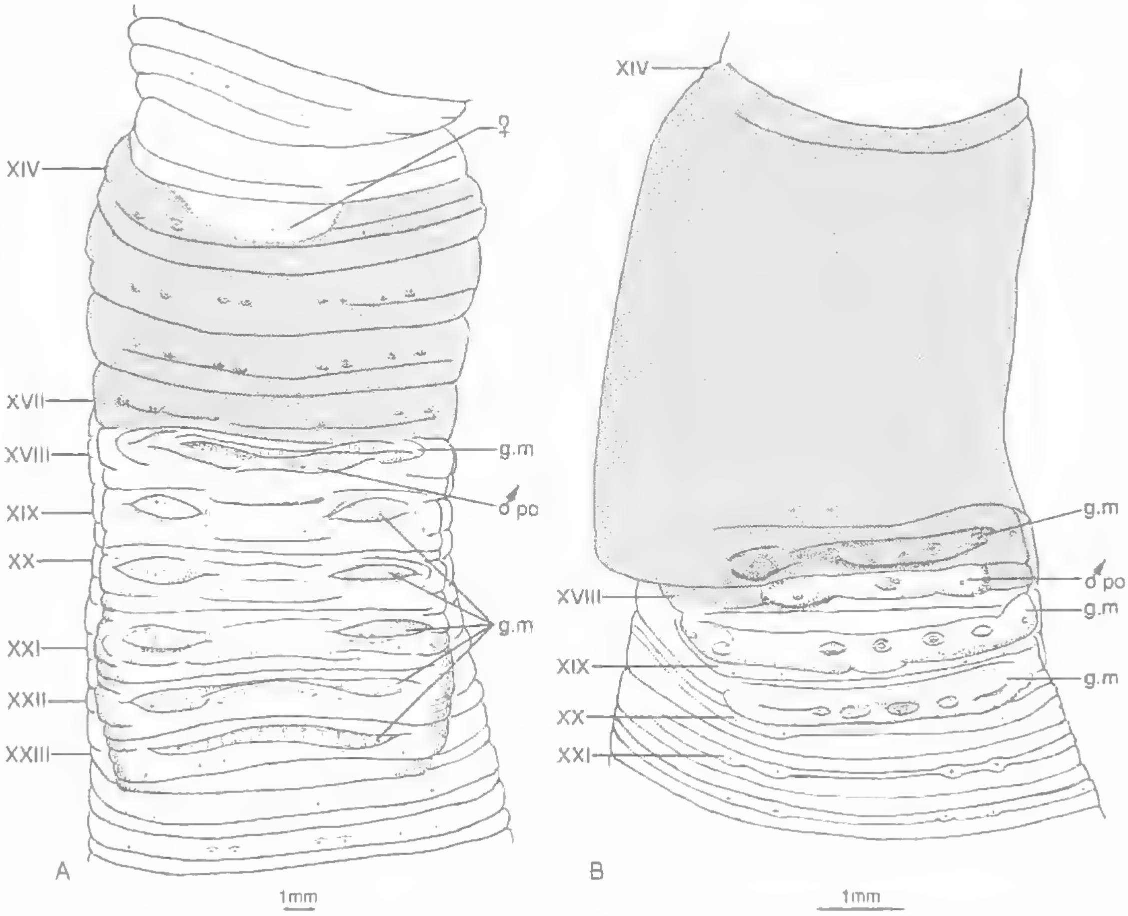

FIG. 1. Genital fields. A, *Perissogaster excavata* (TUGLO specimen); B, *Digaster nemoralis* (paralectotype). Clitellum shaded.

setally. Spermathecal pores not externally visible, in 7/8 and 8/9, appearing from internal examination to lie in *b* lines but stated by Fletcher (1887) to be in *a* lines.

Some preclitellar septa thickened; 9/10-12/13 (-13/14; Fletcher, 1887) immensely strong; tendons connecting the septa, of which those between septum 5/6 anteriorly are very strong. Dorsal blood vessel single, continuous onto the pharynx and passing under the brain. Last hearts in XII, those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in V-IX (IV- IX; Buchanan, 1909) slender and dorsoventral only, though valvular, and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal from 3/4IX to XIII (VIII-XIII; Buchanan, 1909), rudimentary in the last segment; adherent to the oesophagus. A large, free latero-oesophageal trunk present on each side, median to the dorsoventral commissurals in V-IX, ending in the plexus on the floor of the oesophagus in IX and continuous in IV anteriorly as a thick longitudinal ventrolateral parietal trunk. Subneural vessel absent. Oesophagus forming 3 large subspherical strongly muscular gizzards, in V, VI and VII, decreasing in size posteriad, each constricted off from but abutting on the others without appreciable intervention of unmodified oesophagus (connected by short pieces of oesophagus; Fletcher, 1887). The oesophagus simple, lacking calciferous glands, in VIII-XV, though internally with low papillae. Intestine commencing in XVI, muscular thickening, caeca and typhlosole absent. Nephridia meronephridia: tufts of numerous astomate micromeronephridia on and lateral to the pharynx in II, III and IV send composite ducts to the pharynx in III and IV and those of II to the buccal cavity; numerous minute astomate exonephric parietal micromeronephridia in V-XIII, becoming very dense in XIV in which many are, in addition, adherent to the posterior septum; very numerous shortly stalked nephrostomes present on the anterior face of septum 14/15 and apparently arising mostly from the dense bands of exonephric septal nephridia on the posterior face of this septum. Nephridia in XV and succeeding segments dense bands on the anterior and posterior septa, with numerous funnels restricted to the anterior face of the posterior septum; parietal nephridia few but at least some of them with funnels. By XIX the nephridial bodies are chiefly on the posterior face of each septum, with more than 100 stalked funnels on the anterior face of the septum on each side; parietal nephridia are very few. In the caudal region nephridia are dense on the anterior faces of the septa, co-

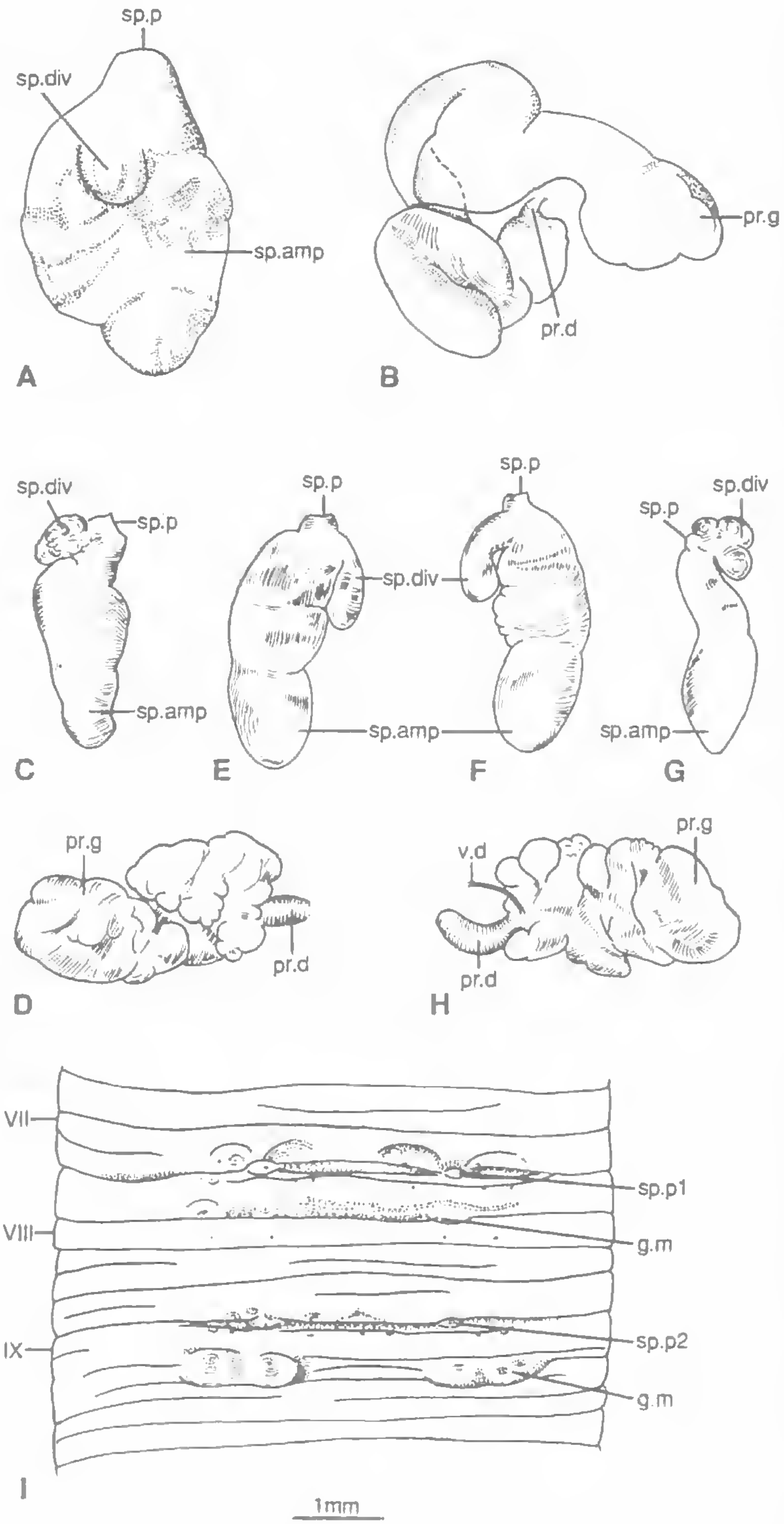

FIG. 2. A,B, *Perissogaster excavata* (paralectotype): A, left spermatheca of IX; B, right prostate. C, D, *Digaster queenslandica* (lectotype): C, left spermatheca of IX; D, left prostate. E-I, *Digaster nemoralis*: E,F, ventral and dorsal views of left spermatheca of IX (lectotype); G, right spermatheca of IX (paralectotype); H, right prostate (paralectotype); I, spermathecal genital field (paralectotype).

existing with numerous stalked funnels and less numerous, with very few evident funnels, on the posterior faces, parietal nephridia are absent; no enteronephry is demonstrable.

Testes and large iridescent funnels in X and XI; testis-sacs absent; seminal vesicles racemose, much divided, in IX and XII, the posterior pair the larger. Prostates (Fig. 2B) tubuloracemose, restricted to an enlarged segment XVIII (or unilaterally in XVIII and XIX; Fletcher, 1887) each basically a broad tortuous tube but with some portions, particularly at the ental end, fused so that the tubular form has in places been lost; almost sessile, the short duct being concealed in the body wall (vas deferens opening into the duct at the base of the gland; Sweet, 1900). Fan-shaped ovaries, and funnels, in XIII. Spermathecae (Fig. 2A) 2 pairs, in VIII and IX, each virtually sessile on the body wall, with flattened ovoid ampulla and short broad diverticulum on its anterodorsal surface, the diverticulum more or less bi- or trilobed.

Digaster Perrier, 1872

D. nemoralis must now be added to the genus, as redefined by Jamieson (1975), as it is here shown to have the dichogastrin condition of the nephridia seen in all species of *Digaster*. The following changes in the definition are necessitated by the present study: *P. queenslandica* must be excluded from the statement that there may be 3 gizzards (see account below). This number is now limited in *Digaster* to *D. nemoralis* and variant individuals (Jamieson, 1963) of *D. perrieri*. The intestinal origin in the genus is now XVI-XIX and absence of a typhlosole is no longer constant as a typhlosole is present in *D. nemoralis*.

Digaster nemoralis (Fletcher, 1889)
(Figs 1B, 2E-I)

Perissogaster nemoralis Fletcher, 1889: 1527-1528.
Digaster nemoralis; Beddard, 1895: 486; Jamieson, 1963: 86; 1971: 75.
Perissogaster nemoralis; Michaelsen, 1900: 198; Jamieson, 1970: 44; 1975: 268-269.

Material Examined

Gosford, New South Wales, 2 clitellate, much dissected type specimens, AMW1438, here designated the lectotype (L) and paralectotype (P).

Description

Length = 90+, 105mm, width (midclitellum) = 5.5mm, greatest width (forebody) = 6mm (lectotype, paralectotype), segments (P) 192. Form circular in cross section. Segments I-III simple; IV biannulate with the setae on the anterior annulus; from V, segments quadriannulate with the setae on the second annulus, and often with faint additional furrows; postclitellar segments triannulate. Pigmentless buff in alcohol. Prostomium broad, prolobous or perhaps slightly proepilobous, it and the peristomium with many longitudinal furrows. Dorsal pores visible posteriorly, location anteriorly indeterminable owing to previous dissection (commencing after about X; Fletcher, 1889). Setae minute, in 8 regular longitudinal rows throughout, commencing on II; setae *a* and *b* replaced by penial setae in XVIII; in XII *aa*:*ab*:*bc*:*cd*:*dd* = 3.25:1.00:3.30:1.94:13.09; circumference = 15.4mm; *dd*:*u* = 0.47. Nephropores not externally recognisable. Clitellum annular, XIV-1/2XVIII; intersegmental furrows, dorsal pores and setae suppressed. Male pores in XVIII (Fig. 1B) on distinct ellipsoidal papillae, in *a* lines; the two papillae medianly conjoined by a transverse boss which widens medianly around a midventral oval pit-like glandular stigma. A median transverse pad present in each of intersegments 17/18, 18/19 and 19/20, each with a transverse series of similar stigmata. Numerous stigmata associated with tumescence (Fig. 2I) also present in VII, VIII and IX in association with the spermathecal pores. Female pores not visible. Spermathecal pores on distinct papillae in 7/8 and 8/9, in *a* lines.

Some preclitellar septa thickened: 5/6-9/10 very strong. Dorsal blood vessel single, anterior course indeterminable owing to previous dissection. Last hearts in XIII; those in X-XIII large and latero-oesophageal, each receiving a broad short connective from the supraoesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in VIII (and IX?; and further anteriorly?) slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supraoesophageal vessel narrow and adherent to the oesophagus but limits indeterminable. Broken latero-oesophageal trunks observed in segment VI. Subneural vessel absent. Oesophagus forming 3 large strongly muscular gizzards, in V, VI and VII, each bowl-shaped and occupying the posterior half of the segment, the oesophagus in the anterior half being similarly dilated but only slightly muscularised. Oesophagus very short, almost suppressed, in VIII; in IX and X short but laterally expanded and in XI-XIV forming paired,very conspicuous, strongly vascularised dilatations, increasing in size posteriorly to very large in XIV; these dilatations dorsolateral, internally with numerous low lamellae but not constricted off from the general oesophageal lumen. Oesophagus in XV and XVI narrow but invaginated into the dilatation in XIV in which it has the appearance of a rosette-like valve. Intestine commencing, with abrupt widening, in XVI; muscular thickening and caeca absent; a deep laminar dorsal typhlosole present. Nephridia meronephridia; large astomate tufts with many spiral loops in II-IV send a common (multiple?) duct forward on each side, traced anteriorly in II but further course indeterminable. Smaller aggregates with lateral outliers in V to VII are restricted to the posterior septum but are exonephric by separate individual ducts, one from each nephidium. By VIII the nephridia form a transverse exonephric band of several moderately large meronephridia at junction of posterior septum and body wall. By XII the band of several nephridia on each side is parietal with the forwardly directed ducts entering the body wall presetally; from XIII there is an increasing tendency for the median nephridia to form diffuse aggregations, though by about XXII these aggregations have reduced to 2 to 3 nephridia lateral to which are 4 smaller nephridia forming regular longitudinal rows; all nephridia are exonephric, avesiculate and apparently astomate. Towards the caudal end there are 3 well spaced nephridia on each side in very straight longitudinal rows lateral to what appear to be two or more aggregated nephridia. In the paralectotype which, unlike the lectotype, is complete posteriorly, the median-most nephridium in several posterior segments has a preseptal funnel and is enlarged as an exonephric megameronephridium. Finally in approximately 7 most posterior segments the regular arrangement of nephridia breaks down, nephridial loops filling the segments transversely and the median nephridium is further enlarged; the lateral nephridia appear to be interconnected by a medianly directed duct; the median nephridium retains the preseptal funnel but whether it and the lateral nephridia are exonephric or enteronephric is indeterminable. Testes and large iridescent sperm funnels in X and XI; testis-sacs absent; seminal vesicles racemose, large, in IX, XI and XII. Prostates (Fig. 2H) racemose; subrectangular deeply incised lobes, with stout moderately long muscular duct which branches within the gland and entally receives the vas deferens. Penial setae slender entally strongly curved needles, the ectal tip delicately pointed with recurved extremity; ectal region with a few fine apically directed spines; a mature seta (paralectotype) 0.96mm long; the shaft 21 µm wide at midlength. Bushy ovaries and funnels, in XIII; ovisacs not recognisable. Spermathecae (Fig. 2E,F,G) 2 pairs, in VIII and IX, each with elongate sacciform to pointed ovoid ampulla which is joined ectally and anteriolaterally by a clavate inseminated diverticulum, duct ectal to the ampulla very short. In the paralectotype the diverticulum is bi- or usually multi-loculate.

Digaster queenslandica (Fletcher, 1889) (Fig. 2C,D)

Perissogaster queenslandica Fletcher, 1889: 1529-1530.

Digaster queenslandica; Beddard, 1895: 485; Sweet, 1900: 124; Jamieson, 1970: 44; 1971: 75; 1975: 268-269.

Perissogaster queenslandica; Michaelsen, 1900: 199; 1916: 22-24.

MATERIAL EXAMINED

Oxley, southeast Queensland, collector T.G. Sloane, AMW1408, two specimens here designated lectotype (L) and paralectotype (P).

DESCRIPTION

Length = 162mm, width at segment XV = 6.5mm, greatest width (forebody) = 8mm, segments 215. Form circular in cross section but with some ventral flattening posteriorly. Segments I to III simple; from IV biannulate with setae on the posterior annulus and sometimes with weaker further annulation; simple from approximately XX posteriorly. Pigmentless buff in alcohol. Prostomium prolobous though longitudinal furrowing of the peristomium perhaps includes a narrow dorsal tongue. Dorsal pores unusually obvious, first in 4/5 but with a rudiment in 3/4. Setae in 8 regular longitudinal rows throughout, *a* and *b* absent in XVIII; in XII, *aa:ab:bc:cd:dd* = 2.57:1.00:2.00:1.78:18.57; circumference = 21.5mm; *dd*: *u* = 0.60. Nephropores not externally recognisable. Clitellum not developed. Male pores in XVIII, in *a* lines, on small almost contiguous papillae. Female pore unpaired in XIV, midway between the setal arc and anterior margin. Spermathecal pores 2 pairs, minute but distinctly visible in VIII and IX, appreciably behind the anterior margin; those in IX 0.55mm apart.

Septa 4/5 and 5/6 fairly strongly thickened; 6/7 and 7/8 slightly thickened; 8/9 moderately strongly; 9/10-13/14 strongly thickened, 11/12-13/14 especially so. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a slender connective from the dorsal vessel but otherwise unbranched; commissurals in (V?) VI-IX slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal vessel well developed in X-XII, weakly developed in IX and 1/2XIII. A large latero-oesophageal trunk on each side median to the commissurals joining the supra- oesophageal vessel in X and traceable forward at least to VI. Subneural blood vessel absent. Oesophagus with only 2 gizzards (contrary to Fletcher, 1889), in VI and VII, each very large, strongly muscular and subcylindrical, abutting on each other with almost inappreciable intervening oesophagus; that in VI preceded in the anterior portion of the segment by unthickenened oesophagus. The oesophagus in V dilated to almost the size of a gizzard but its musculature unthickened, a spurious impression of a gizzard being produced by the ensheathing muscular septum 5/6. Dilatation and vascularisation of the oesophagus in XIV-XVI but no calciferous glands. Intestine commencing in XVIII; muscular thickening absent; caeca and typhlosole not recognisable but maceration precludes certainty. Nephridia all avesiculate meronephridia: dense aggregations of meronephridial tubules on the parietes in II-IV appear exonephric but tubules adherent to the pharynx are possibly enteronephric; from V to the anterior intestinal region astomate, avesiculate micromeronephridia scattered on the parietes, the nephridia decreasing in size and becoming more numerous (many) posteriorly; never forming regular longitudinal rows. Caudally, in the last approximately 18 segments, with 15-20 astomate parietal micromeronephridia in transverse single file on each side lateral to an exonephric(?) megameronephridium with large preseptal funnel. Testes and funnels in X and XI, funnels in XI larger and iridescent; seminal vesicles large, racemose, in XI and XII. Prostates (Fig. 2D) depressed elongate tongue-shaped, sufficiently incised to be considered racemose but with a main, central canal from which many lesser side branches supply the lobes; ectal duct short, weakly muscular and largely concealed in loose parietal musculature. Penial setae absent. Ovaries presumably represented by a pair of large depressed lobes with no evident oocytes on the anterior septum of XIII; funnels on the posterior septum. Spermathecae (Fig. 2C) 2 pairs, in VIII-IX, each with conical-ovoid ampulla and short, wide duct: which is joined anterolaterally by a compact inseminated internally multiloculate and externally slightly lobed diverticulum.

REMARKS

The demonstration above that Fletcher and Michaelsen were incorrect in recognising a third gizzard in this species gives unexpected support to the author's contention (Jamieson, 1970) that the previously described anatomy and the hitherto unrecognised dichogastrin condition of the nephridia warranted placing it in *Digaster*.

Michaelsen (1916) recorded this species from Brisbane, southeast Queensland.

CLADISTICS

As an adjunct to taxonomic considerations of the status of *Perissogaster* the relationships of the three species formerly placed in the genus to each other and to *Digaster* and *Didymogaster* have been investigated, using the PAUP program of Swofford (1990), version 3.0s, using 30 characters for 25 species (Jamieson, unpublished). Suffice to say the exhaustive and branch-and-bound search options gave a very large number of trees with grossly discordant topologies and that a consensus tree gave no resolution beyond separating the two *Didymogaster* species as the sister-group of the *Digaster-Perissogaster* assemblage. This assemblage formed a single polytomy. Many of the characters proved highly homoplasic.

A subset of 15 of the less noisy characters applied to only 11 taxa, consisting of a hypothetical ancestor (hypanc), the three *Perissogaster* species, the two *Didymogaster* species, and representatives of the *lumbricoides* and *perrieri* groups within *Digaster* (details below) produced a single tree (Fig. 3) in a branch-and-bound search. In view of the discordant results when the full character-taxon set is used, or when additional taxa are added to the reduced set, this single tree can be regarded as only one of many objective hypotheses of relationships. It is possible that the true phylogeny is not recoverable from the morphology of extant species of the total assemblage. The single tree obtained will, nevertheless be used in the following 'intuitive' discussion of

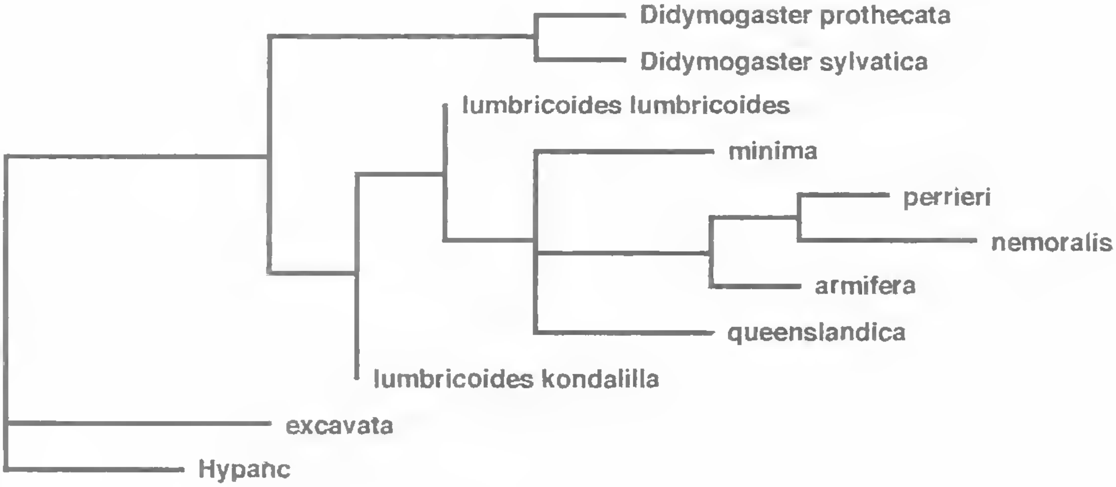

FIG. 3. Single tree obtained for 11 taxa indicated, and 15 characters, using the branch-and-bound option of the PAUP program. Tree length = 27. Consistency index (CI) = 0.778. Homoplasy index (HI) = 0.222. CI excluding uninformative characters = 0.667. HI excluding uninformative characters = 0.333. Retention index (RI) = 0.684. Rescaled consistency index (RC) = 0.532

relationships and in support of the taxonomic decision made.

An ancestor (hypanc) with a single gizzard and other characters indicated in the matrix was envisaged. Recourse, alternatively, to using the more objective out-group strategy, using *Didymogaster* as the outgroup, gave similar results.

CHARACTERS EMPLOYED

This list is a subset of those used in the more comprehensive analysis. As a result some of the characters (marked #) are uninformative or invariable. *Numbers are deducted from the states of some characters to limit their values to less than 10 and avoid hexadecimal notation.

#1. Male pore(s) unpaired 1; paired 2.
2. Female pore(s) unpaired 1, paired 2.
#3. Spermathecal pore(s) unpaired 1, paired 2.
4. First spermathecal segment.
5. Spermathecal pores, number of transverse sets.
6. Segment (-10) of last hearts.*
7. First gizzard segment.
8. Number of gizzards.
9. Caudal preseptal funnels 1, many 2.
10. Testes in X 1, X and XI 2, XI 3.
11. Seminal vesicles in IX, X, XI and XII 1, IX and XII 2, XI and XII 3, XII 4, IX, XI and XII 5.
12. Prostates tubular 1, tubuloracemose 2, racemose 3, racemose- bipartite 4.
13. Penial setae absent, 0 present 1.
#14. Number of diverticula per spermatheca.
15. Diverticula uniloculate 1, multiloculate 2.

INPUT DATA

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Taxon                                123456789012345
Didymogaster prothecata              222643621224011
Didymogaster sylvatica               222733621224011
Digaster lumbricoides
                 lumbricoides        22282262?233011
                 kondalilla          22282262?234011
            minima                   22282262?343012
            perrieri                 2?282352?233111
            queenslandica            212822621232012
            nemoralis                2?2823531253112
            armifera                 22282252?223112
Perissogaster excavata               222822532222011
Hypanc                               2225525112?1?11
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BRANCH-AND-BOUND SEARCH SETTINGS

Initial upper bound: unknown (compute via stepwise).
Addition sequence: furthest.
Initial MAXTREES setting = 100.
Branches having maximum length zero collapsed to yield polytomies.
Topological constraints not enforced.
Trees are unrooted.
Multi-state taxa interpreted as uncertainty.
Outgroup = Hypanc.
Characters were all scored as unordered and unweighted.

DISCUSSION

From 'intuitive' taxonomic considerations, *Perissogaster nemoralis* and *P. queenslandica* are here included in *Digaster* because of the correlation of three points: general anatomy, multiplication of gizzards and dichogastrin nephridia. The dichogastrin nephridial condition occurs in earthworm genera of several zoogeographical regions of the world and has been accompanied by multiplication of the gizzard, from the usual monogastric condition, independently in the various regions. It has been argued (Jamieson, 1975) that the di- or trigastric condition in Australian earthworms originated in what is now the montane coastal province of the Eastern Sub-region, to which such forms are restricted, independently of evolution of this condition in other, non-Australian zoogeographic regions.

Multiplication of gizzards might have developed only once (strict monophyly) or in more than one lineage predisposed to this development by virtue of genetic similarity and relationship (parallelism or homoplasy). It is unlikely that a third hypothesis, development of the multigastric condition independently in unrelated taxa, is tenable as this would presuppose edaphic or other environmental factors favouring repeated development of the condition in the montane coastal province but absent from other provinces.

The taxa with multiple gizzards are (1) a large group of species, containing the type species, *D. lumbricoides* with two gizzards, in VI and VII, which is restricted to Queensland and northern New South Wales; (2) *D. perrieri* and *D. armifera*, with two gizzards, in V and VI, allopatric in New South Wales; (3) two species, comprising the genus *Didymogaster*, with the *lumbricoides* location of the gizzards, sympatric with *D. perrieri* and *D. armifera* in central New South Wales; and (4) the three species of *Perissogaster* s.lat., *P. excavata*, *P. nemoralis* and *P. queenslandica*.

With regard to the phylogenetic validity of these four groupings: on the basis of gizzard location the *lumbricoides* group might reasonably be assumed to form a monophyletic group. However, neither the restricted PAUP analysis (Fig. 3) nor analysis of the full taxon-character set supported monophyly.

Digaster perrieri and *Digaster armifera*, though sympatric with *Didymogaster*, differ from other *Digasters* and from *Didymogaster* in having gizzards in V and VI, and might be considered the sister-group of the *lumbricoides-Didymogaster* group. However, PAUP analyses do not support a monophyletic *perrieri-armifera* assemblage (Fig. 3).

Didymogaster has various conflicting positions in the PAUP analyses, including that of sister-group to *Digaster*, as shown in Fig. 3. Synapomorphies defining *Didymogaster* include intrasegmetal location of spermathecal pores and presence of testic-sacs (neither character used in the restricted analysis). Its generic status is accepted here.

The relationship of the three former *Perissogaster* species may now be further considered. It has been shown that *Perissogaster queenslandica* is digastric, contrary to previous descriptions, with the *lumbricoides* location of the gizzards, in VI and VII and is placeable in *Digaster*, as supported in Fig. 3 and advocated by Jamieson (1970, 1971). *P. nemoralis*, sympatric with *D. armifera* and *D. perrieri*, is here transferred to *Digaster* as its only trigastric species (excepting variant individuals of *D. perrieri*). Consideration has been given to the possibility that the *armifera-perrieri* condition (gizzards in V and VI) and *lumbricoides* condition (gizzards in VI and VII or their homeotic equivalent) have developed dichotomously from the trigastric condition seen in *nemoralis*. It has been shown above that cladistic analysis does not support recognition of either group. Conversely, the trigastric condition might be considered to reflect a further development of the propensity in *Digaster* to thicken the oesophageal musculature in two of segments V to VII. The PAUP analyses support the latter view, presenting the trigastric condition as an apomorphy of *nemoralis* developed from the digastric condition of an ancestral *Digaster* perhaps (Fig 3) shared with *D. perrieri*.

The relationships of the type species of *Perissogaster*, *P. excavata*, are especially uncertain. If multiple gizzards are evidence of relationship, it would appear that multiplication of nephrostomes characteristic of *P. excavata*, which would formerly have assigned it to the tribe Megascolecini sensu Jamieson (1971), has occurred in this species independently of acquisition of this condition in other genera of the tribe. This would support the author's contention that the Megascolecini may represent a grade rather than a clade. The anatomy of *P. excavata* is close to that of *P. nemoralis*, excepting the nephridial condition, extending to the origin of the intestine in XVI, unknown elsewhere in *Digaster*. However, an intuitive postulate of a sister-group relationship of *excavata* to the *Digaster-Didymogaster* assemblage is supported by the restricted PAUP analysis (Fig. 3). It is equivocal as to whether the common ancestor of *excavata* and this assemblage had two or three gizzards despite indicating independent origin of three gizzards in *nemoralis* from the digastric condition. The common ancestor of *excavata* and the *Digaster-Didymogaster* assemblage is computed to have had the dichogastrin condition of nephridia (single preseptal funnel on each side), retained as a plesiomorphy in *Digaster* but changing to the multifunnelled condition in *excavata*. Some trees from the larger data set nevertheless do associate *excavata* and *nemoralis* as sister-species within the *Digaster* assemblage.

The PAUP analyses are not sufficiently extensive to rule out the alternative possibility that *Perissogaster excavata* is descended from a monogastric megascolecin ancestor with its nephridial condition of multiple preseptal nephrostomes in caudal segments, conditions seen in *Oreoscolex* Jamieson. Two *Oreoscolex* species from New South Wales, *O. illawarrae* (Fletcher, 1889) and *O. saccarius* (Fletcher, 1886) agree with *P. excavata* in having the intestinal origin in XVI. However, confinement of multiplication of gizzards to a single zoogeographical province favours the view that multiplication is a rare apomorphy more likely to occur in closely related forms than in forms as distinct as *Oreoscolex*.

In view of the logical and computational ambivalence as to the position of *P. excavata* it is here considered that taxonomic convenience is best served by retaining this species in the monotypic genus *Perissogaster*. This has been redefined in the taxonomic section.

ACKNOWLEDGEMENTS

The author is grateful to Dr C.N. Smithers for providing new material of *P. excavata*. This work was made possible by Australian Biological Resources Study and Australian Research Council support.

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